MORPHOLOGICAL AND GEOGRAPHICAL DISJUNCTIONS IN FORMS OF *EUCALYPTUS NITIDA* Hook. f. (MYRTACEAE): WITH SPECIAL REFERENCE TO THE EVOLUTIONARY SIGNIFICANCE OF BASS STRAIT, SOUTHEASTERN AUSTRALIA

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Abstract: Variation in seedling characters of *Eucalyptus nitida* (shining peppermint) and related species was analysed phenetically using multivariate classification and ordination techniques. The principal aims were to clarify the identity of the peppermint species occurring on some Bass Strait islands and to examine patterns of variation in seedling morphology across the geographic range of populations currently referred to *E. nitida*. Related species were included as aids to interpreting patterns. Analyses were based on seedling and juvenile foliage, the latter resolving the taxa more completely. On the basis of seedling morphology, Bass Strait island peppermint appears to be conspecific with Tasmanian *E. nitida*, and these populations appear to be separate from Victorian and South Australian populations currently referred to *E. nitida*. It is suggested that the degree of distinctness is sufficient to warrant separate taxonomic recognition of the Australian mainland populations.

Systematic affinities of Tasmanian peppermints are discussed, and an explanatory hypothesis is proposed to account for the present distribution of peppermint species and the high degree of endemism among Tasmanian peppermints.

Current usage recognizes six species of *Eucalyptus* as occurring variously on the larger islands of Bass Strait (Table 1). This contrasts with about 75 species in Victoria and 25 on the Tasmanian mainland. Five of the six species belong to the informal subgenus *Symphyomyrtus* as recognized by Pryor and Johnson (1971) and are relatively widespread on both sides of Bass Strait. They are *E. viminalis* Labill., *E. dalrympleana* Maiden, *E. globulus* Labill., *E. ovata* Labill. and *E. brookerana* A. M. Gray. Apart from the occurrence of *E. globulus* on Rodondo Island just south of Wilsons Promontory (Kirkpatrick *et al.* 1974), these species are confined to the seven largest islands.

The sixth species, *E. nitida* Hook. f., is a member of the peppermint group of eucalypts and is placed in the informal subgenus *Monocalyptus* (Pryor & Johnson 1971). It is considered to occur not only on the Tasmanian mainland but also in far southeastern South Australia, in scattered localities close to the coast of Victoria from the South Australian border to Sperm Whale Head, and in the Grampians (Willis 1970) (Fig. 1). In recent years, the name has been applied to populations of Bass Strait island peppermint (e.g. Curtis & Morris 1975). These populations occur on all the larger islands, on some smaller islands of the Furneaux Group and on two islands of the Kent Group, Deal and Dover Islands.

Willis (1972, p. 416) described all the above populations as "undoubtedly conspecific". Previously, Victorian and South Australian populations were known variously as *E. dives* (e.g. Ewart 1930, Hall *et al.* 1963), *E. vitrea* (e.g. Black 1964, Boomsma 1972, Parsons *et al.* 1972) and *E. radiata* (e.g. Parsons 1966). Similarly, island populations had been given names of Tasmanian mainland species such as *E. tenuiramis* (e.g. Brett 1938), *E. simmondsii* (e.g. Jackson 1965, Hall *et al.* 1970, Hope 1973) and *E. amygdalina* (Hope 1973).

Significantly, Blakely (1934, 1965) applied the name *E. tenuiramis* Miq. to specimens collected from Deal and Flinders Islands which he had sighted at the National Herbarium of New South Wales. Willis (1967) strongly disagreed with the application of this name, mainly on the ground that the glaucousness of leaves and buds described by Miquel has not been found to occur in any Bass Strait island specimens. The name *E. tenuiramis* has since been applied strictly to lowland populations from southeastern Tasmania having connate juvenile leaves and a dense waxy bloom on shoots, buds and fruits. Subsequently, Willis (1970) reduced *E. simmondsii* of northwestern Tasmania to synonymy with *E. nitida* and made his claim for conspecificity, but without offering any reasons for his decisions.

With the other five island species occurring on both sides of Bass Strait, the notion of a comparable distribution for *E. nitida* is plausible. However, there are two *prima facie* reasons why Willis's claim should not be accepted uncritically: firstly, of the four systematic groups of eucalypts that occur in Tasmania, the peppermints show the highest degree of endemism (Table 2); secondly, variation within *E. nitida sensu* Willis is considerable, particularly with respect to habit and bark type, fruit size and shape, and juvenile leaf and stem morphology.

Bass Strait island peppermint is generally a small tree, dominant in low open-forest communities; it is 2 to 10 m tall, of poor form, sometimes multi-stemmed, and has smooth bark with a short, scaly to sub-fibrous butt; the more or less flat-topped turbinate to pyriform fruits are relatively large (to 9 mm wide); coppice leaves are ovate, sessile and opposite for many pairs. Herbarium specimens conform reasonably well with the type specimens of *E. nitida* which were collected from several Tasmanian mainland localities. The nearest Victorian
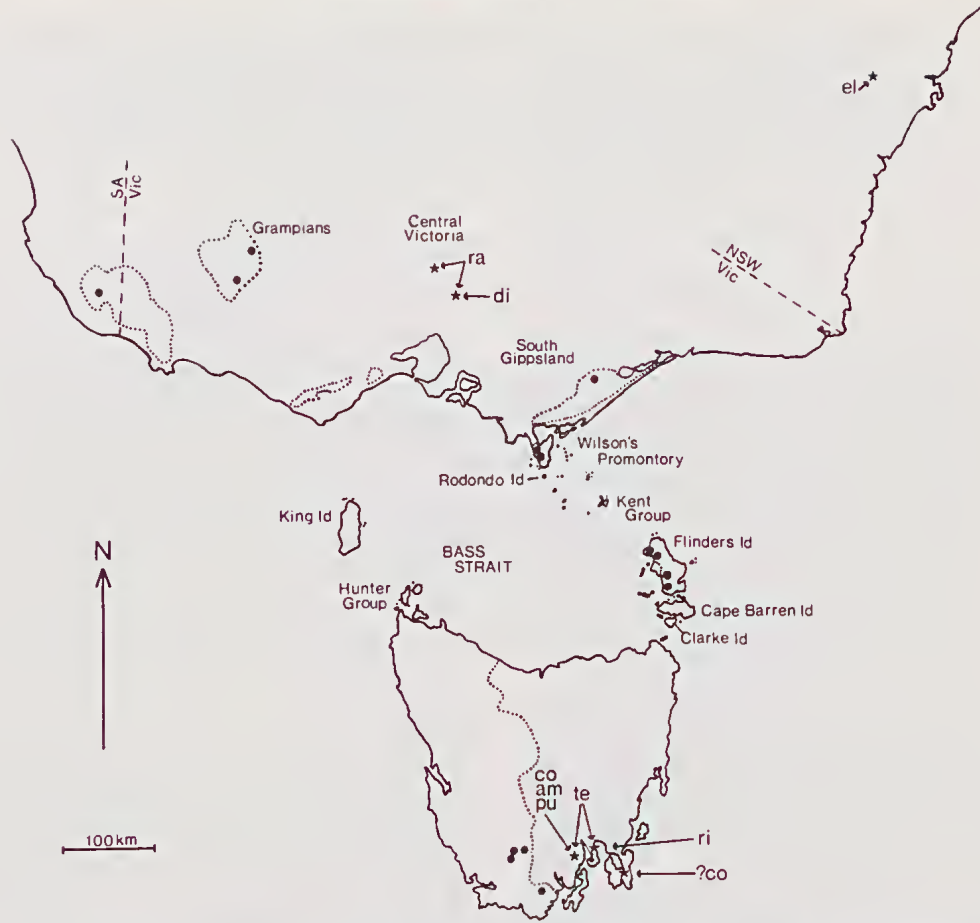
Fig. 1—Generalised distribution limits of *E. nitida sensu* Willis and localities of seed collections: *E. nitida* (•), other species (*). Abbreviations: am = *E. amygdalina*, co = *E. coccifera*, di = *E. dives*, el = *E. elata*, n = *E. nitida*, pu = *E. pulchella*, ra = *E. radiata*, ri = *E. risdonii*, te = *E. tenuiramis*.

populations of peppermint currently referred to *E. nitida* occur on Wilsons Promontory, but they differ from island peppermint in several respects: bark is rougher, buds and fruits are smaller, and coppice leaves are lanceolate.

In some parts of its range, Tasmanian *E. nitida* is not separable from *E. amygdalina* (Hall *et al.* 1963, A. Gray pers. comm.). Some Victorian and South Australian populations include trees of intermediate status and bearing some resemblance to *E. radiata* (Parsons *et al.* 1977) or *E. pauciflora* (Willis 1970, Boomsma & Lewis 1980). Throughout the geographic range, there appear to be few readily interpretable disjunctions in adult form that might clarify the taxonomy.

The diagnostic importance of juvenile leaves has been recognized for almost a century (Maiden 1922). More recently, Brooker (1979) observed that seedling morphology can be an extremely valuable aid in assigning species to series within the genus *Eucalyptus*. Ladiges *et al.* (1981) found that differences in seedling morphology between *E. ovata* and *E. brookerana* were sufficient to justify recognition of these taxa at the specific level. It was therefore considered desirable to

use seedling characters to test the adequacy of *E. nitida sensu* Willis, principally with respect to Bass Strait island populations. A seedling trial was established in a uniform environment to examine the patterns of variation in seedling morphology within *E. nitida sensu* Willis, and to assess the distinctness of *E. nitida* seedlings with respect to those of related species.

Related species were considered to be all the members of subseries *Amygdalininae* of series *Piperitae* (Pryor & Johnson 1971). Details of their geographic and altitudinal distributions, growth forms and bark types are summarized in Table 3. Typically, they occur on infertile, acidic soils derived from sedimentary, metamorphic or granitic parent materials; average annual rainfall ranges from 600 to 1300 mm. The member species are distinguished from other members of the subgenus *Monocalyptus* on the basis of possessing some combination of the following characters (modified from Wilcox 1979):

1. "Peppermint" bark—finely textured, shortly fibrous, loosely coherent rough bark which persists on larger branches.

TABLE 1

OCCURRENCE OF *Eucalyptus* SPECIES ON THE ISLANDS OF
BASS STRAIT

Island	Area (km²)	Species					
		vim	dal	glo	ova	bro	nit
King Island	1,100	+	−	+	−	+	− *
Hunter Group							
Hunter Island	70				+		+
Three Hummock Island	68				+		+ ?
Robbins Island	96				+		+
Furneaux Group							
Flinders Island	1,333	+	+	+	+	−	+
Cape Barren Island	450	+		+	+		+
Clarke Island	75	+		+	+		+
Prime Seal Island	10						+
Babel Island	4						+
Great Dog Island	3						+
Kent Group							
Deal Island	15						+
Dover Island	2.5						+
Erith Island	3.0						−
Rodondo Island	0.8			+			

vim = *E. viminalis*, dal = *E. dalrympleana*, glo = *E. globulus*,
ova = *E. ovata*, bro = *E. brookerana*, nit = *E. nitida*.
+ = present, − = notably absent.

* The map provided by Jackson (1965) showing *E. nitida* (syn.
E. simmondsii) as occurring on King Island is considered to
be incorrect (P. Barnett, King Island, pers. comm.)

2. Seedling leaves opposite and sessile for first 4 to 6
nodes; juvenile leaves opposite and sessile for an
indefinite number of following nodes.
3. Verrucae (protruding oil glands) on margins and
midribs of seedling and juvenile leaves, and on
seedling stems.
4. Characteristic essential oils in juvenile and mature
foliage, particularly piperitone, phellandrene and
cineole.
5. Mature leaves symmetrical, with more or less
longitudinal secondary venation, and with the
apex acuminate or hooked.
6. Buds numerous, clavate and pedicellate; capsules
pyriform-turbinate with a flattened disc.

The following taxa were omitted from the study: (1) *E.
radiata* ssp. *robertsonii sensu* Johnson & Blaxell (1973)
occurring in upland areas of New South Wales and Vic-
toria; (2) *E. robertsonii sensu* Jackson (1965) and Hall *et
al.* (1970) considered by Johnson & Blaxell (1973) to be
an undescribed subspecies of *E. amygdalina*; and (3) the
two species that form subseries *Piperitinae* of series
Piperitae (Pryor & Johnson 1971) considered by
Brooker (1977) to be better classified with the ash group
of eucalypts (series *Obliquae* subgenus *Monocalyptus*).

METHODS

SEED COLLECTION AND SEEDLING GROWTH

Of the nine species included in the seedling trial,
eight were represented by seed collections from in-
dividual mother trees. *E. nitida sensu* Willis was
represented by seed collected from five trees on Dover
Island, six on Flinders Island, four in southern
Tasmania, two each on Wilsons Promontory and in the
Grampians, and one each in South Gippsland at Bellbird
Swamp near Longford and in southeastern South
Australia near Wandillo (Fig. 1). *E. tenuiramis* and *E.
radiata* were represented by seed from two trees each; *E.
dives*, *E. pulchella*, *E. amygdalina* and *E. risdonii* by
seed from one tree each; all these trees were considered
to be typical members of each taxon and accordingly
were located in southeastern Tasmania or central Vic-
toria. The subalpine Tasmanian species *E. coccifera* was
represented by seed from one tree considered to be
typical and from one tree representing a population con-
sidered to be anomalous on the basis of both adult mor-
phology and its lowland locality (Devil's Kitchen,
Tasman Peninsula). The ninth species, *E. elata*, was
represented by seed obtained through the Forests Com-
mission of Victoria from the vicinity of Nerriga, N.S.W.
It is not known whether the seed was from a single tree
or was pooled from several trees. Voucher specimens
from the parent trees of all species except *E. elata* are
held in herbaria: MELU or FRI.

Seed was germinated on moist filter paper in petri
dishes. Young seedlings were pricked out into plastic
buckets containing a general purpose potting mix and
were allowed to grow in a heated glasshouse for seven
months. Initially, each bucket contained six seedlings
from one seed collection; after three months, these were
thinned out to the most robust three per bucket. This
growth system was chosen to suit the scale of the trial
while providing sufficient replication and a reasonable
volume of soil for individual seedlings. The trial was ter-
minated when competitive effects on growth rate (ex-
pressed as shoot height) became apparent in some
buckets, causing a reduction in the number of assessable
seedlings.

PHENETIC ANALYSIS OF SEEDLING CHARACTERS

Individual seedlings were subject to multivariate
analysis of morphological characters. Following the
distinction made between seedling and juvenile leaves by
Blake (1953) and Chippendale (1973), two data matrices
were prepared. The first was based on seedlings after
four months' growth; seedling leaf characters were
assessed on one of the paired leaves at the third node
above the cotyledonary node and the matrix incor-
porated data from 96 seedlings using 35 characters
(Table 4). The second matrix was based on seedlings
after seven months' growth. Juvenile leaf characters
were assessed on one of the paired leaves at the seventh
node, or at the next highest node at which a clear change
to juvenile foliage had occurred. The matrix incor-
porated data from 85 seedlings using 36 characters.
Changes in the character set used for the second matrix
were due to changes in seedling morphology with age.

Table 2

Tasmanian Species of *Eucalyptus*. Geographic and Systematic Distribution

(compiled primarily from Pryor and Johnson 1971)

Species	Tas.	S.A.	Vic.	N.S.W.	Qld.	Systematic Group
E. delegatensis	+		+	+		Subg. *Monocalyptus*
E. obliqua	+	+	+	+	+	Sect. *Renantheria*
E. pauciflora	+	+	+	+	+	Series *Obliquae*
E. regnans	+		+			
E. sieberi	+		+	+		
E. amygdalina	+					Subg. *Monocalyptus*
E. coccifera	+					Sect. *Renantheria*
E. nitida	+	+ ?	+ ?			Series *Piperitae*
E. pulchella	+					Subseries *Amygdalininae*
E. risdonii	+					
E. tenuiramis	+					
E. barberi*	+					Subg. *Symphyomyrtus*
E. brookerana*	+		+			Sect. *Maidenaria*
E. ovata	+	+	+	+	+	Series *Ovatae*
E. rodwayi	+·					Subseries *Ovatinae*
E. cordata	+					Subg. *Symphyomyrtus*
E. dalrympleana	+		+	+		Sect. *Maidenaria*
E. globulus	+		+	+		Series *Viminales*
E. gunnii	+					
E. morrisbyi	+					
E. perriniana	+		+	+		
E. rubida	+	+	+	+		
E. urnigera	+					
E. vernicosa	+					
E. viminalis	+	+	+	+	+	

* Tentative placement of *E. barberi* Johnson and Blaxell and *E. brookerana* A. M. Gray after Ladiges *et al.* (1981).

Each raw data matrix was analysed separately using classification and ordination programs from CSIRO's TAXON P2 package as follows: data were input to the polythetic program MSEUC which produces an inter-element dissimilarity matrix from mixed data using a squared Euclidean metric with Burr's standardization (see Williams 1976). The dissimilarity matrix was then input to SAHN which generates a hierarchy based on "distances" between individuals (seedlings). Output from this agglomerative procedure was restricted to the last 14 fusions (15 groups). Group data were then input to the diagnostic programs GPCOM and CRAMER to assist in interpreting relationships between groups and the characters that contributed to their formation. An inter-group dissimilarity matrix was generated using GPDIS and input to the ordination program PCOA which finds principal coordinates for group centroids. The inter-group dissimilarity matrix was also input to MST which calculates a minimum spanning tree linking "nearest" group centroids (see Gillison 1978). Groups were also redefined using GPRES and input to BACRIV which calculates correlation coefficients between characters and the vectors (axes) generated by PCOA. Output from both MST and BACRIV assists in interpreting the ordinations. Further details of these methods can be obtained from CSIRO Division of Computing Research.

RESULTS

The limited size of the seedling trial, especially with respect to species represented by progeny from only one or two trees, necessitates caution in interpreting the analyses. Only the broader elements of the patterns found will be discussed, and only then in relation to interpreting variation within *E. nitida sensu* Willis.

Seedling Leaf Analysis

The classification based on seedling leaves produced a major dichotomy separating Victorian and South Australian seedlings of *E. nitida* from Bass Strait island seedlings (Fig. 2). Tasmanian mainland seedlings occurred equally on both sides of the dichotomy, reflecting the extent of their variability. Moreover, classification to the 15-group level did not produce a clear separation of some *E. nitida* seedlings from those of three other species: Group 2 incorporated seedlings of *E. dives* with *E. nitida* from the Grampians and South Gippsland; Groups 3 and 4 incorporated *E. radiata* with *E. nitida* from Wilsons Promontory and South Gippsland; and Groups 6 and 7 incorporated *E. coccifera* with *E. nitida* from Flinders Island and the Tasmanian mainland. Ten of the 15 groups included some representatives of *E. nitida*.

The characters contributing most to the major dichotomy in the classification were those related to leaf

TABLE 3

Tasmanian Peppermints and their Allies (Subseries *Amygdalininae*)

(Compiled primarily from Hall *et al.* (1970), Willis (1972), Curtis and Morris (1975))

Species	Geographic distribution	Altitudinal range	Typical habit	Bark type
E. coccifera	Tas. Central Highlands. Sub-alpine.	600-1500 m	Shrub to small tree 1-6(-12) m	Smooth
E. risdonii	Tas. Restricted to a small area near Hobart.	Near sea level to 150 m	Shrub to small tree 3-8(-20) m	Smooth with circular scars
E. tenuiramis	Tas. South-eastern quarter.	Near sea level to 450 m	Tree 10-30 m	Smooth with circular scars
E. pulchella	Tas. South-eastern quarter.	150-550 m	Tree 10-30 m	Smooth with ± subfibrous butt
E. amygdalina	Tas. Eastern half.	Near sea level to 850 m	Tree 15-35 m	Peppermint — variable
E. nitida	Tas. Western half; Bass Strait islands. Vic. Patchy, southern coast, Grampians S.A. Extreme south-east.	Near sea level to 850 m	Small to medium tree (5-)10-20(-35) m	Variable. Typically sub-fibrous on trunk, but may be smooth-barked
E. radiata	Vic. Widespread in Central Highlands and foothills. N.S.W. Eastern third.	150-1200 m	Tree 15-35 m	Peppermint
E. dives	As for *E. radiata*, but on drier sites.	150-120 m	Tree 10-30 m	Peppermint to larger branches
E. elata	Vic. Far east coast, Macalister R. valley. N.S.W. South east coast. All alluvial sites.	Near sea level to 200(-750) m	Tree 20-35(-50) m	Smooth with sub-fibrous butt

shape (principally the ratio of length to maximum width) plus the occurrence of verrucae on leaf margins (Table 5). Another leaf shape ratio (LM:LL), internode length, stem glaucousness and leaf colour were important in producing the next two dichotomies. Taking only those ten groups that incorporated *E. nitida*, the four mainland groups (1-4) included seedlings that had green, ovate to lanceolate leaves with acute apices; internodes were relatively long; verrucae were absent from the leaf margins. The six groups that incorporated island and Tasmanian *E. nitida* (5-10) included seedlings with green to blue-green, broadly ovate leaves; apices were more or less obtuse; internodes were relatively short; and verrucae were conspicuous on the margins of all seedlings in these groups. The last-mentioned character clearly separated all Tasmanian and island seedlings of *E. nitida* from all Australian mainland seedlings, including those from Wilsons Promontory. Together with the presence of more or less undulate margins, these glands were most prominent in progeny of trees from Dover Island in the Kent Group.

Ordination of the group centroids together with links between nearest neighbours are shown in Fig. 3. The first three axes (vectors) accounted for 64.4% of the total variation in the data matrix. The relative positions of group centroids confirmed the pattern of clear separation between Victorian and South Australian seedlings of *E. nitida* (Groups 1-4), and Bass Strait island and some Tasmanian mainland seedlings (Groups 5-9). The remaining Tasmanian mainland seedlings (Group 10) occupied an intermediate position with respect to the characters separating the groups on axis 1. These included the same characters that produced the major dichotomy in the classification. Axis 2 was most strongly correlated with internode length and total height and the extreme position of Group 10 suggests that some Tasmanian mainland populations may have an inherently slow growth rate relative to other populations of *E. nitida*, at least during early growth.

JUVENILE LEAF ANALYSIS

The classification based on juvenile leaves again produced a major dichotomy separating Victorian and South Australian samples of *E. nitida* from both Bass Strait island and Tasmanian mainland populations (Fig. 4). All seedlings of *E. nitida* were contained within seven groups and were clearly differentiated from all other species included in the trial. To that extent, the analysis based on juvenile leaf characters produced a more readily interpretable result.

The characters contributing most to the major dichotomy in the classification were again principally related to leaf shape; in addition, secondary vein angle and oil gland density were important (Table 6). Leaf colour and the ratio of length from leaf base to widest point over total length were important in producing the next two dichotomies respectively. Taking only those seven

TABLE 4

SEEDLING CHARACTERS SCORED FOR DATA MATRICES

Binary

1. Leaf margin (*S*) ....revolute/not
2. Leaf margin...........................undulate/not
3. Verrucae on stem ....present/absent
4. Verrucae on abaxial midrib ....present/absent
5. Verrucae on leaf margin ....present/absent
6. Stem..............................glaucous/not
7. Lignotuber ....present/absent
8. Petiole (*J*) ....present/absent
9. Leaf lamina (*J*) ....concolorous/discolorous

Multistate

10. Leaf base shape.........acute/obtuse/cordate/connate
11. Leaf angle to stem ....< 80°/80-100°/ > 100°
12. Leaf margin ...entire/repand/sparsely serrulate/serrulate
13. Leaf colour ....yellow-green/green/blue-green/glaucous
14. Midrib colour ....yellow/pale red/intense red
15. Margin colour.............yellow/pale red/intense red
16. Stem colour...............yellow/pale red/intense red
17. Anthocyanin on abaxial leaf surface (*S*)......absent/pale
/intense
18. Leaf orientation (*J*) ....horizontal/twisted/vertical

Numerical

19. Leaf length (= LL) (mm)
20. Maximum leaf width (= MW) (mm)
21. Width 5 mm from leaf base (= WB) (mm)
22. Width 5 mm from leaf apex (= WA5) (mm)
23. Width 10 mm from leaf apex (= WA10) (mm)
24. Leaf length from base to widest point (= LM) (mm)
25. Total height (= TH) (mm)
26. Length 3rd or 7th internode (= IL) (mm)
27. Mean internode length (= ML) (mm)
28. Leaf apex angle (°)
29. Secondary vein angle (°)
30. Total number of leaf pairs (*J*)
31. Number of leaf pairs opposite
32. Leaf thickness (mm $\times 10^2$)
33. Oil gland density (per cm^2)
34. Ratio LL:MW
35. Ratio LM:LL
36. Ratio WB:MW
37. Ratio WA5:WA10
38. Ratio height to 3rd node:TH (*S*)
39. Ratio IL:ML

S = scored only for the matrix based on seedling leaves at
third node.
J = scored only for the matrix based on juvenile leaves at
seventh or higher node.

groups that incorporated *E. nitida*, seedlings in the two Australian mainland groups had predominantly green linear to lanceolate leaves with extremely acute apices; secondary vein angles approached semi-longitudinal; oil gland density was high, especially in Group 2 from Wilsons Promontory and South Gippsland. Seedlings in the five island and Tasmanian mainland groups had more or less elliptical, green to blue-green leaves with correspondingly higher apex and secondary vein angles; oil gland density was relatively low to zero. Interestingly, the trend in oil gland density appears to be the

reverse of that reported by Ladiges *et al.* (1981) for *E. ovata* and *E. brookerana*; that is, within *E. nitida sensu* Willis, values were higher at lower latitudes and low at higher latitudes.

Ordination of the group centroids together with links between nearest neighbours are shown in Fig. 5. The first three axes (vectors) accounted for 66.6% of the total variation. The relative positions of the group centroids again confirms the pattern of clear separation between Groups 1 and 2 incorporating seedlings from the Australian mainland, and Groups 3 to 7 incorporating all island and Tasmanian seedlings. As indicated by both the classification and the nearest neighbour linkages, Group 2, incorporating *E. nitida* from Wilsons Promontory and South Gippsland, is more similar to Group 14 incorporating *E. radiata* than it is to Group 1 incorporating *E. nitida* from the Grampians and South Australia. This is principally due to differences expressed on axis 3, notably in oil gland density. Axis 1 was correlated most strongly with a number of characters relating to leaf shape; axis 2 was correlated positively with internode length and negatively with total number of leaf pairs.

Comparison of the two analyses indicates that, at least on the basis of seedling morphology, Bass Strait island peppermint populations are phenetically most closely related to the Tasmanian species *E. nitida sensu stricto*. The patterns of variation in seedling morphology suggest that island and Tasmanian mainland populations are distinguishable from Australian mainland populations currently referred to *E. nitida*, principally on the basis of (1) leaf shape and presence or absence of verrucae on seedling leaf margins apparent in seedling 3 to 4 months old and (2) leaf shape and oil gland density apparent in juvenile leaves of seedlings 6 to 7 months old.

DISCUSSION

TAXONOMIC IMPLICATIONS

Since *E. nitida* is the only peppermint species considered to occur on both sides of Bass Strait at present, the disjunctive variation pattern within that species means that all Australian mainland peppermint populations can be distinguished from all Tasmanian and island populations, regardless of any taxonomic difficulties that may occur within those regions. The intermediate geographic position of Wilsons Promontory might reasonably lead to the expectation that its peppermint populations have some intermediate taxonomic status. However, results of the present study plus preliminary results of a study of adult morphology suggest that the resemblance with *E. radiata* is paramount.

The discontinuous pattern of variation within *E. nitida sensu* Willis suggests that consideration should be given to recognizing new taxa. In particular, it would appear that there are grounds for recognizing populations of peppermint occurring in western Victoria including the Grampians and in southeastern South Australia at the species level. As indicated by Pryor and

TABLE 5

SEEDLING LEAF ANALYSIS

MEANS AND FREQUENCIES (%) FOR THE SEVEN CHARACTERS THAT CONTRIBUTED MOST TO THE FIRST THREE DICHOTOMIES IN THE HIERARCHICAL CLASSIFICATION (a) AND IN THE TEN GROUPS INCORPORATING SEEDLINGS OF *E. Nitida sensu* WILLIS (b)
Group numbers and combinations are those indicated in Fig. 2. Numbers of seedlings are shown in brackets.

Characters	(a) Group Combinations		(b) Groups incorporating *E. nitida sensu* Willis									
	1+2+3+ 4+10+11 +12	5+6+7+ 8+9+13 +14+15	*Vic., S.A. groups*				*Bass Strait island, Tas. groups*					
1st dichotomy			1	2	3	4	5	6	7	8	9	10
	(39)	(57)	(6)	(7)	(6)	(8)	(21)	(5)	(5)	(8)	(6)	(6)
Seedling leaf apex angle (°)	60	85	65	73	52	53	83	84	96	84	77	67
Ratio seedling leaf length: maximum width	2.9	1.8	2.9	2.0	2.7	2.9	1.9	1.6	1.5	1.7	1.9	2.7
Verrucae on seedling leaf margin	28%	95%	0	0	17%*	12%*	100%	100%	100%	100%	100%	100%
2nd dichotomy	1+2+3+4	10+11+12										
	(27)	(12)										
Ratio seedling leaf length from base to widest:total length	0.25	0.48	0.37	0.26	0.18	0.18	0.34	0.29	0.28	0.30	0.25	0.45
Length 3rd internode (mm)	39.7	18.6	47.3	46.6	35.7	31.0	33.5	26.2	32.0	27.6	20.7	13.0
3rd dichotomy	5+6+7+ 8+9+13	14+15										
	(48)	(9)										
Stem glaucousness	0	100%	0	0	0	0	0	0	0	0	0	0
Seedling leaf colour— green	'65%	0	100%	100%	100%	100%	71%	20%	80%	100%	0	0
blue-green	35%	33%	0	0	0	0	29%	80%	20%	0	100%	100%
glaucous	0	67%	0	0	0	0	0	0	0	0	0	0

* contributed by *E. radiata* only.

Johnson (1971), the name "*E. vitrea*" may not be available for these populations because the type specimen is believed to be of hybrid origin, the putative parental species being *E. radiata* and *E. pauciflora* (series *Obliquae*). It is nonetheless possible that *E. pauciflora* may have been involved in the evolution of what appears now to be a stable taxon (Boomsma 1972). Seedlings and coppice foliage from present-day populations in western Victoria and southeastern South Australia have certain ash-like characters, notably the tendency of juvenile leaves to be falcate and to be oriented in the vertical plane due to twisting of petioles.

SYSTEMATIC AFFINITIES

Blakely (1934) placed the nine species represented in this study in three subseries of peppermints based principally on juvenile leaf shape. *Angustifoliae* included *E. pulchella, E. elata, E. radiata, E. amygdalina* and *E. nitida; Latifoliae* included *E. nitida* (as *E. simmondsii*), *E. dives* and *E. coccifera*; and *Connatae* included *E. tenuiramis* and *E. risdonii*. The first two of these subseries incorporated species from both sides of Bass Strait. Pryor and Johnson (1971) fused Blakely's three subseries into one (*Amygdalininae*), but they recognized

two superspecies. The first included *E. risdonii* and *E. tenuiramis* and corresponds to Blakely's subseries *Connatae*. These two species are morphologically similar in several important characters (such as having connate juvenile foliage), and moreover, in terms of geographic range, the distribution of the former is contained within the distribution of the latter. Their relative positions in the analyses reported here lend weight to the view that they are sufficiently closely related to justify grouping in a superspecies. The second superspecies recognized by Pryor and Johnson (1971) included *E. radiata, E. amygdalina* and *E. nitida*. None of the analyses reported here linked any of the three possible species pairs, let alone all three together in one group; that is, resemblances based on seedling morphology appear to be relatively weak or lacking. The justification for grouping these three species into a superspecies appears therefore to warrant further examination.

If Australian mainland populations currently referred to *E. nitida* are to be treated as taxonomically separate at the species level from Tasmanian and island populations, then all Tasmanian peppermints would be endemic (Table 2). This degree of endemism may prove
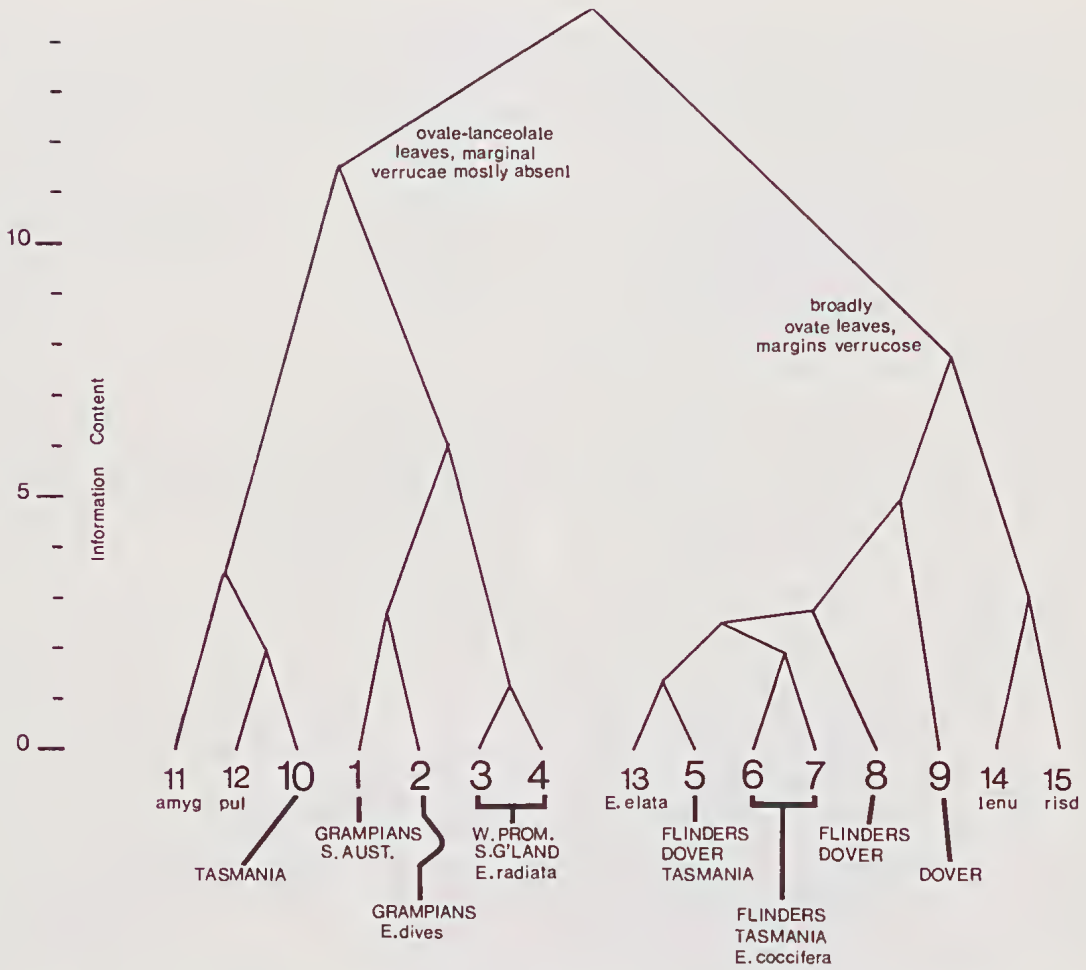
Fig. 2 — Seedling leaf analysis. Hierarchical classification of 96 seedlings based on leaf morphology at the third node and truncated at the 15-group level. Groups 1-10 incorporate seedlings of *E. nitida sensu* Willis. Abbreviations: amyg = *E. amygdalina*, pul = *E. pulchella*, risd = *E. risdonii*, tenu = *E. tenuiramis*.

to be of systematic and phylogenetic significance. The present study placed considerable emphasis on continuously varying morphological characters relating particularly to leaf shape and such manifestations as apex angle and base shape. It is therefore not surprising that various combinations of these characters were important in the analyses and that the major dichotomies did not correspond to the major geographic disjunction that is Bass Strait. Juvenile leaf shape appears to be a plastic character likely to vary over a wide range of more or less related systematic groups within the genus. Its systematic and evolutionary significance is difficult to elucidate; there are, for instance, no broad-scale patterns sifting broad- and narrow-leaved species of *Eucalyptus* into particular climatic or edaphic zones (contrast leaf orientation). An alternative approach emphasizing discretely varying characters may indicate grounds for treating the Tasmanian peppermints as a distinct systematic group, possibly a subseries within a peppermint series.

Evolutionary Significance

More than 50% of Tasmanian eucalypts are considered to be endemic (Table 2); this contrasts with only 8% of Victorian species. An explanatory hypothesis is required that will account for the present distribution of *E. nitida* and phenetically related species whilst recognizing the high degree of endemism among Tasmanian peppermints.

The islands of Bass Strait are considered to be remnants of a land bridge connecting the Australian mainland to Tasmania (Jennings 1971). During the Pleistocene, the land bridge formed with each period of glaciation and associated lowering of sea level. It is estimated that Tasmanian temperatures would have been about 5°C lower than at present, and the tree-line would have been as low as near present sea level on the west coast to 4-500 m above sea level on the east coast during periods of glaciation (Galloway 1965, Macphail 1979). Forests, woodlands, and scattered trees would
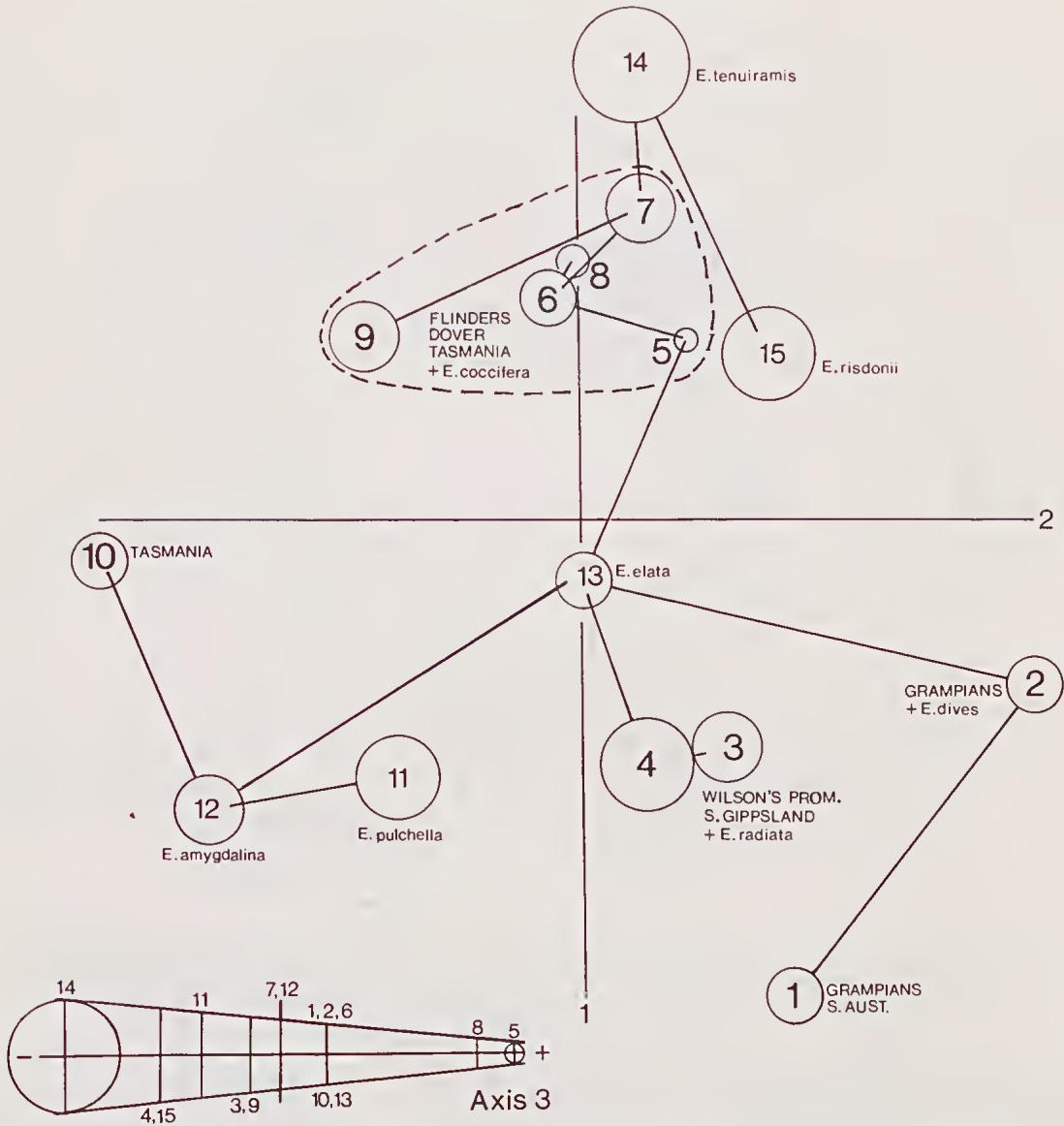
Fig. 3—Seedling leaf analysis. Ordination of group centroids and links between nearest neighbours. Groups as indicated in Fig. 2. Axis 3 is represented as the diameter of spheres (following Gillison 1978).

have been restricted to a coastal fringe, to the central midlands of Tasmania and to the land bridge (J. Hope 1973, G. Hope 1978, Macphail 1979). At the time of maximum glaciation during the late Pleistocene, open grassland communities with scattered eucalypts would have been widespread in southeastern Australia including the low-lying central part of the land bridge (Hope 1978). Outcropping granite hills that form the present islands of Bass Strait may have provided refuges for *Eucalyptus* forest communities as suggested by Ladd (1979) for the granite highlands of Wilsons Promontory. The most recent interruption of the land bridge to form Bass Strait probably occurred between 12 000 and 13 500 years ago (Jennings 1971, Hope 1973), initially

separating Tasmania from the Australian mainland to the north of King and Flinders Islands and probably the Kent Group.

During interglacial periods when Bass Strait reformed, selection pressures may have resulted in divergence and speciation. During subsequent periods of glaciation, boundaries of Tasmanian eucalypt species probably shifted northward, mainly in response to climatic constraints. New habitats would have become available to lowland species as the islands increased in size and coalesced in sequence from south to north to form land corridors through both eastern and western ends of Bass Strait. As the land bridge formed, probably by connecting the eastern land corridor to Wilsons Pro-
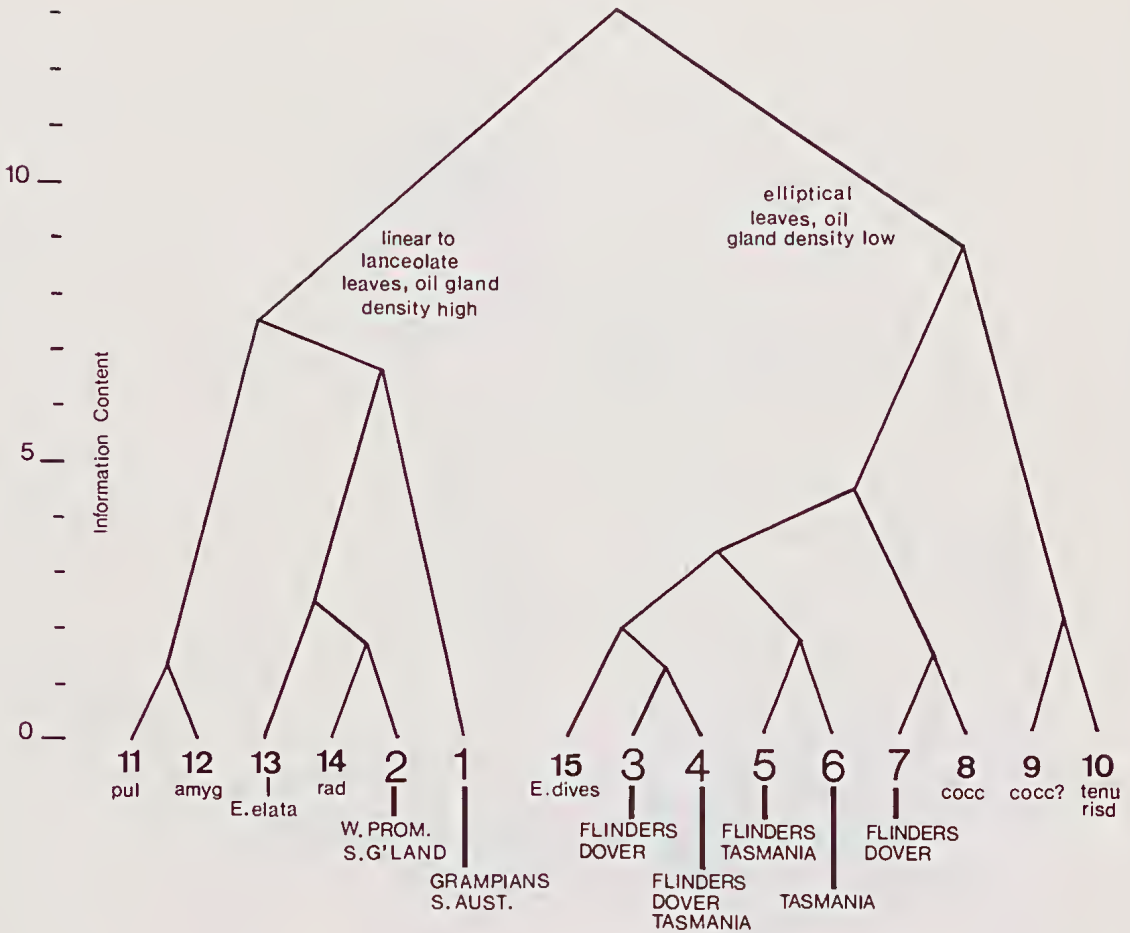
Fig. 4 — Juvenile leaf analysis. Hierarchical classification of 85 seedlings based on leaf morphology at the seventh or higher node and truncated at the 15-group level. Groups 1-7 incorporate seedlings of *E. nitida sensu* Willis. Abbreviations: amyg = *E. amygdalina*, cocc = *E. coccifera*, pul = *E. pulchella*, rad = *E. radiata*, risd = *E. risdonii*, tenu = *E. tenuiramis*.

montory, northbound species occupying the land corridor may have met more widely tolerant southbound species capable of migrating against the climatic gradients into new habitats. Genetic isolation may or may not have been complete, depending on the degree of divergence that had occurred among related species (or populations) during the previous interglacial period of geographic isolation. The subsequent rise in sea level and loss of suitable habitats would, perforce, lead to the contraction of species boundaries both north and south, and may have left relatively few species able to survive on the islands of the Strait. But it may have lead to new opportunities for divergence and speciation, and geographic and phylogenetic origins may become obscured.

The distribution of *E. nitida sensu stricto* in Tasmania and on some islands of Bass Strait parallels that reported by Hope (1973) for many members of the vertebrate fauna. Following her interpretation, it is suggested that the extent of phenetic similarity between island and Tasmanian mainland populations of the species may be taken to indicate the degree of genetic isolation of that species at any time when it may have been in contact with related species migrating southward on the land bridge. If present island populations of *E. nitida* were to be intermediate between Tasmanian and Australian mainland species or populations, this would suggest that, during the last period of glaciation, populations originating from either side of the Strait and meeting on the land bridge were not reproductively isolated. We report here evidence that, at least with respect to seedling morphology, island populations are not only more similar to Tasmanian mainland populations than they are to any other population or species represented in this study, but also are not intermediate between Tasmanian and any Australian mainland populations currently referred to *E. nitida sensu* Willis. The extent of the disjunction implies at least a degree of genetic isolation, if not complete isolation. In so far as island populations differ from Tasmanian mainland populations, some divergence may have occurred since the sea-level rose isolating the present islands; alter-
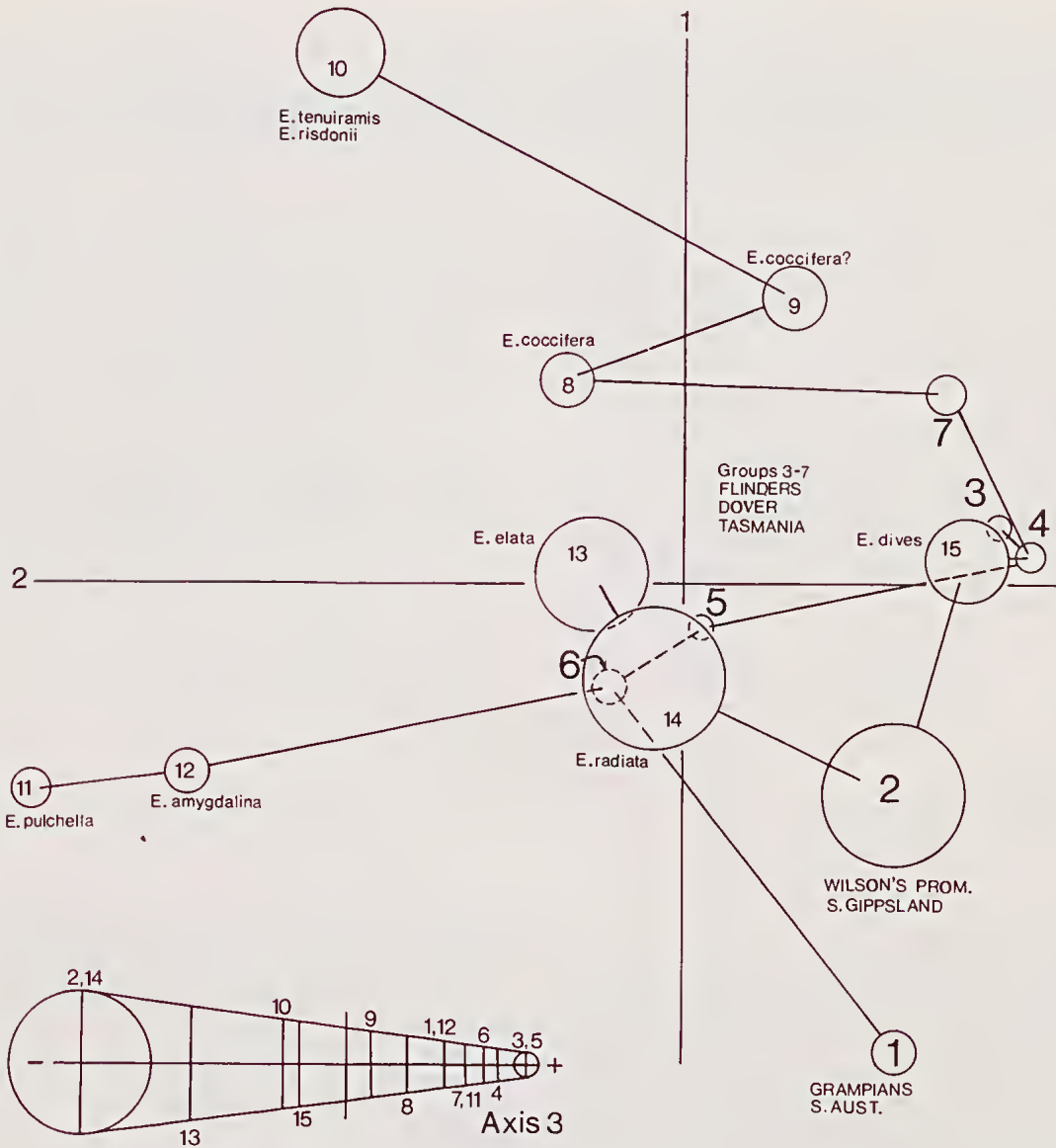
Fig. 5 – Juvenile leaf analysis. Ordination of group centroids, and links between nearest neighbours. Groups as indicated in Fig. 4. Axis 3 is represented as the diameter of spheres (following Gillison 1978).

natively, the rising sea may have disrupted a clinal sequence of variation, the island populations being at the northern end of a gradient. This study provides no way of choosing between these two options.

Australian mainland peppermint species and populations may have had various origins. Some may have originated from one or more ancestral species in response to directional selection pressures on the mainland. Others may have resulted from back-migration following radiation in Tasmania.

Further studies are in progress testing the hypotheses outlined above. These will involve sampling on a population basis, taking account of adult morphology and applying the methods of phylogenetic systematics

and variance biogeography as described by Wiley (1980). In the lattermost context, it is of interest that *E. nitida* appears to be absent from the present native flora of King Island while the tall, well formed species, *E. brookerana*, has not been recorded on Flinders Island. This pattern parallels that described for some members of various vertebrate groups (summarized by Hope 1973) and has been attributed principally to higher rainfall on the western side of land bridges formed during the Pleistocene. In contrast, Tasmanian eucalypt species that occur on both islands are geographically widespread on the Australian mainland (*E. viminalis, E. globulus* and *E. ovata*), again resembling some vertebrate distribution patterns.

TABLE 6

Juvenile Leaf Analysis

Means and frequencies (%) for the Seven Characters Contributing Most to the First Three Dichotomies in the Hierarchical Classification (a) and in the Seven Groups that Incorporated Seedlings of *E. nitida sensu* Willis (b)
Group members and combinations are those indicated in Fig. 4. Numbers of seedlings are shown in brackets.

Characters	(a) Group Combinations		(b) Groups incorporating *E. nitida sensu* Willis						
			Vic., S.A. groups		*Bass Strait island, Tas. groups*				
	1+2+11+ 12+13+14	3+4+5+6+ 7+8+9+10 +15	1	2	3	4	5	6	7
1st dichotomy	(31)	(54)	(8)	(8)	(14)	(9)	(7)	(2)	(4)
Secondary vein angle (°)	28	46	28	30	43	47	50	49	35
Apex angle (°)	26	64	28	25	53	58	72	54	42
Ratio juvenile leaf length: maximum width	7.3	2.6	6.0	6.0	3.0	3.0	2.2	3.4	5.0
Maximum juvenile leaf width (mm)	11.3	20.9	14.5	14.0	21.1	21.1	24.7	15.6	10.0
Oil gland density (per cm²)	505	88	279	1012	88	171	92	32	0
2nd dichotomy	3+4+5+6+ 7+8+15 (41)	(13)	9+10						
Juvenile leaf colour — yellow-green	15%	0	0	0	0	0	0	0	0
green	63%	8%	63%	100%	86%	89%	14%	0	100%
blue-green	22%	23%	37%	0	7%	11%	86%	100%	0
glaucous	0	69%	0	0	7%	0	0	0	0
3rd dichotomy	1+2+13+14	11+12							
Ratio juvenile leaf length from base to widest point over total length	0.22	0.55	0.36	0.17	0.26	0.33	0.38	0.44	0.26

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